Factors affecting the local distribution of the Long-tailed Duck *Clangula hyemalis* in Baltic offshore waters

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Abstract

The Long-tailed Duck *Clangula hyemalis* is the main offshore wintering seaduck species in the Baltic region, although numbers have declined steeply since the early 1990s. The reasons for the decline are not well understood and information about habitat choice is scarce. Blue Mussels *Mytilus edulis* are the main food source for Long-tailed Ducks in the southern Baltic Sea and here we have used both modelled and measured raw data on *Mytilus* abundances, patchiness and various bathymetric parameters to study Long-tailed Duck habitat preferences. Long-tailed Ducks were most abundant at depths of 10–30 m and in areas of high *Mytilus* densities. Patchiness of the resource was also very influential, especially when overall *Mytilus* densities were low. Bird abundance was intermediate to high in areas of low patchiness and low where *Mytilus* patchiness was high. This suggests that the birds seek areas that optimise their feeding efficiency.

Key words: Baltic Sea, habitat selection, local distribution, Long-tailed Duck, *Mytilus edulis*, optimal foraging theory.

The Long-tailed Duck *Clangula hyemalis* is the predominant seaduck of the Baltic Sea, especially in offshore waters, with the "Status of wintering Waterbird populations in the Baltic Sea" (SOWBAS) survey estimating that 1,480,000 individuals from the West Siberian/North European Population occurred in the region during 2007–2009 (Skov *et al.* 2011). This represents a marked decrease of approximately 65% since the previous large-scale survey in winter 1992/93 (Durnick *et al.* 1994; Nilsson 2012).

A range of studies have reported on the feeding ecology and spatial distribution of Long-tailed Ducks across the Baltic Sea (Nilsson 1972, 1980a,b; Bräger *et al.* 1995; Stempniewicz 1995; Zydelis & Ruskyte

2005). However, because the majority of Long-tailed Ducks are found over offshore banks in the central parts of the Baltic Sea and spatiotemporal data on their main food source, the Blue Mussel *Mytilus edulis* are generally lacking, few studies have attempted to assess habitat selection explicitly in relation to the distribution and density of their food supply (but see Vaitkus & Bubinas 2001).

Intensive studies on the habitat selection and feeding ecology of marine diving ducks and seaducks, including Long-tailed Ducks were undertaken in southern Sweden during the 1960s and the early 1970s, focussing on the coast of Scania and the vast offshore areas of the Hanö Bight (Nilsson 1972, 1980a). During the years 2007–2012, offshore surveys were once more undertaken in the Hanö Bight in connection with a national monitoring programme of Swedish offshore waters and intensive studies of the marine environment of the area within the MARMONI Project (Ahlman *et al.* 2014). The latter project also included surveys of the benthic communities in the same areas covered by the aerial bird censuses.

In the present contribution we compare the benthic surveys with the bird counts to identify which factors are important for influencing the local distribution and habitat selection of Long-tailed Ducks. In particular, we compare the distribution of wintering Long-tailed Ducks with the distribution and abundance of their favourite food, the Blue Mussel.

Study area

The study area was in the Hanö Bight, in the southern part of the Baltic Sea (mid-point: 55°54 N, 14°30 E, with a ~50 km radius) (Fig. 1). The area borders the Swedish counties of Scania in the south and Blekinge in the north. The region is characterised by shallow depths (< 34 m), an exposed coastline and substrates ranging from sand to large boulders. In the southern part of the area the shore-line consists of sandy beaches with a sandy sea floor in the shallower areas but with a lot of smaller and larger boulders further out at sea. A low salinity of between 7–8 ‰ typifies the marine waters in the Hanö Bight.

In the southern part of the Hanö Bight there is a ridge of moraine (Kiviksbredan) with large boulders and shallower water stretching for some distance parallel with the shore at a distance of more than 10 km from the shore. Another series of moraine ridges are found in deeper water in the northeast corner of the Hanö Bight (at Hanöbankarna). These banks are quite barren in contrast to Kiviksbredan.

Blue Mussels are common throughout the coastal areas in the Hanö Bight but the species is particularly widespread and found at greater densities on the large and relatively shallow flat ridge that extends from Kiviksbredan in the south to Hanöbankarna in the north.

Material and methods

Aerial surveys of Long-tailed Ducks

In the 2007–2012 survey the offshore areas were surveyed by line transects from an aircraft. Transects were laid out so that all important water areas were covered out to a depth of about 30 m. The distance between survey lines was 2 km; layout of the transect

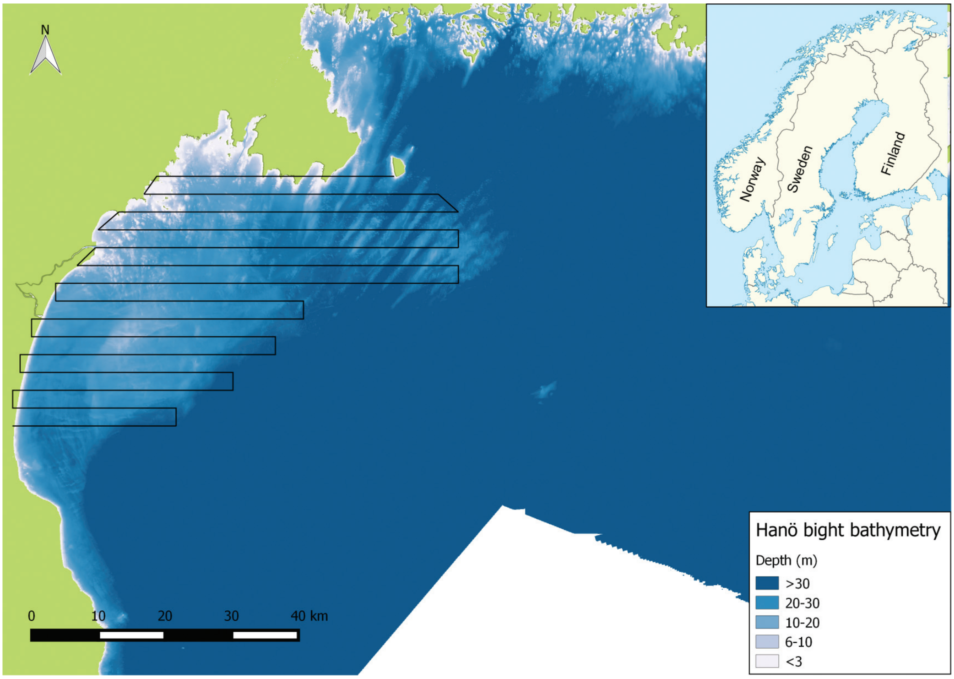

Figure 1. Depth distribution in the Hanö Bight. Lines show the aerial transects.

lines is shown in Figure 1. Surveys were undertaken from a high-winged twin-engine Cessna 337 Skymaster aircraft with good visibility. Flying altitude was at *c.* 70 m and the speed was 150–180 km/h (*i.e.* the slowest possible). Aerial surveys were undertaken only in good weather conditions. Fixed waypoints at the ends of each transect were established and navigation was undertaken with the aid of the aircraft's GPS. Another GPS recorded the actual flight path taking positions every ten seconds. Two observers counted from each side of the aircraft. All observations were recorded electronically with time and were later transferred to a database with the GPS positions.

All waterbirds were counted, and the species recorded, within a strip-transect survey zone extending 200 m from either side of the aircraft. The total width covered for each transect was 320 m, but this included a blind band out to 40 m from either side of the transect line beneath the aircraft where the birds could not be seen. We did not use distance sampling to cover areas further away from the aircraft, but all observations of flocks outside the main survey zone were recorded as additional observations. We therefore assumed that all waterbirds were detected within the areas covered by the strip-transect survey zone.

Counts from the strip-transects were used to estimate regional totals for the different species, using the numbers recorded within the main survey zones and a factor based on the coverage of the different regions (6.25 in this case). The positions of the aircraft were established every ten seconds, meaning that the counting units were approximately 500 m long and 320 m wide. In total, seven aerial surveys were undertaken in the offshore areas during the present study. In earlier years, surveys of Long-tailed Ducks and other seaducks in the area were made by boat, following the methods described by Nilsson (1980a, 2012).

Underwater video surveys

During the period 3 August 2011 to 12 October 2012 underwater submersible video was used to observe and record the substrate class (hard or soft bottom), substrate type (boulder, stone or sand) and percentage cover of *Mytilus edulis* per substrate class. Stratified random sampling was used to select 254 stations within the study area, each with an area of ~25 m^2 surveyed. The cameras used were the Sea Trex HD Underwater Point of View Camera System (STHD) and the Sea-Viewer Sea-Drop camera. Depth was also measured at each station using an echo-sounder. In addition, *Mytilus* percentage cover, substrate and depth data from 78 sampling stations collected between 2006 and 2012 were used to complement the dataset. These data were obtained by diving, snorkelling or wading with an aqua-scope, and were collected as part of local and national monitoring programmes. However, because the main purpose of these surveys was to monitor aquatic vegetation, the stations were mostly allocated to areas with a water depth < 10 m.

Environmental parameters and statistical treatment

To investigate the relationship between habitat parameters and Long-tailed Duck abundance we used bathymetric parameters such as the mean slope of the sea bed and the mean water depth (depthMN) obtained from bathymetric models of the area (Ahlman *et al.* 2014). Mean *Mytilus* coverage (mytMN) and a measure of patchiness (coefficient of variation; mytCV) were included in the analyses, either as raw data from the various monitoring surveys or as modelled parameters (Ahlman *et al.* 2014).

The use of a dataset with modelled predictors permitted the inclusion of data where bird observations were present but data on *Mytilus* abundance or bathymetry were missing or sparse.

Data handling

To obtain the explanatory variables, we used modelled data on *Mytilus* coverage and bathymetry, developed for the "Innovative approaches for marine biodiversity monitoring and assessment of conservation status of nature values in the Baltic Sea" (MARMONI) project, at a 50 × 50 m spatial resolution across the study area. A detailed description of the modelling procedure can be found in Ahlman *et al.* (2014). From these data we calculated the mean *Mytilus* coverage, the corresponding coefficient of variation, and the bathymetric parameters within a circular buffer zone (2 km radius) surrounding the centroid of each 500 × 320 m bird counting unit along the aerial transect (Fig. 2); these measures were then used as explanatory variables in the analyses.

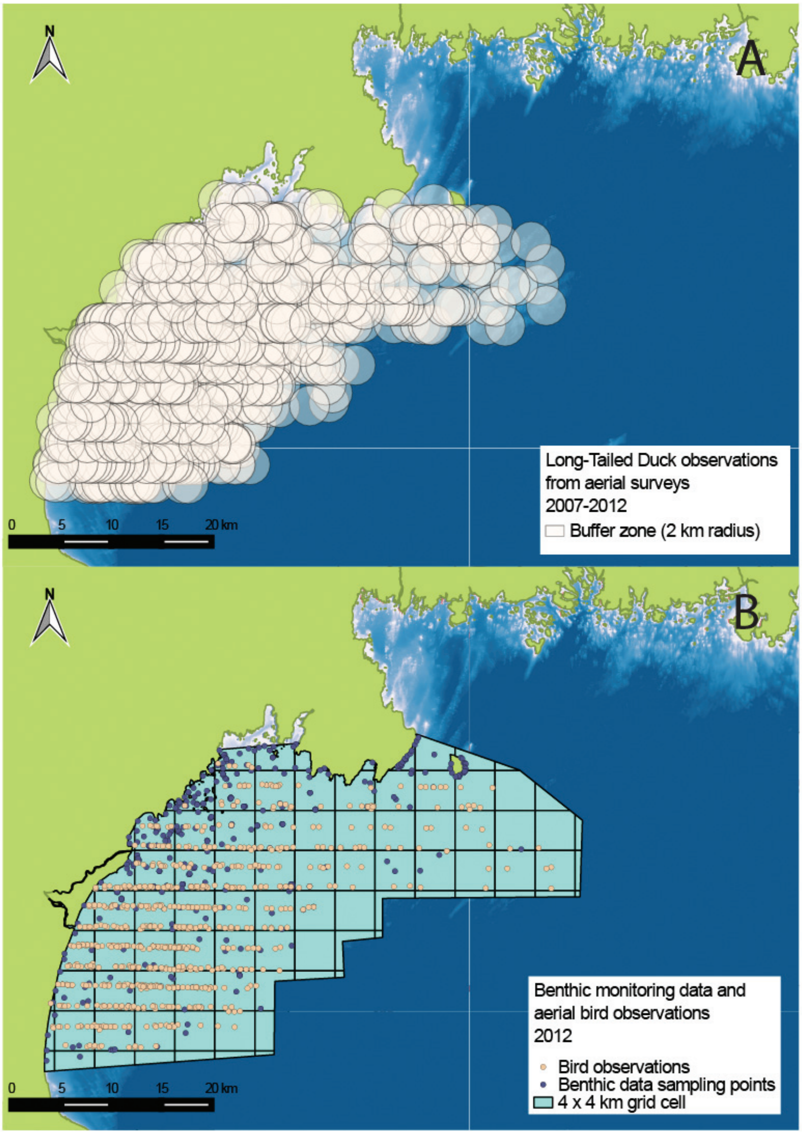

Figure 2. Maps of the study area showing sampling design used to collect data for the models predicting Long-tailed Duck (LTD) densities. Panel A shows LTD observations from 2007–2012 with a 2 km radius buffer zone around each observation to which overlapping, modelled benthic parameters were extracted. LTD absences are not shown for practical reasons but were inter-spaced between shown presences and used in the statistical modelling. Panel B shows the same LTD observations as Panel A but with additional benthic monitoring data collected in 2012. In this case, the mean abundance of LTD was related to the mean or coefficient of variation benthic parameters within individual cells.

The response data included both bird presences and absences in the 500 m transect sections recorded in 2007–2012 inclusive. Moreover, to avoid *Mytilus* and bathymetric data typical for areas where birds were absent to be shared with areas where they were present, we excluded all data within buffer zones containing no birds (*i.e.* absence data) intersecting with presences (buffer zones were partially overlapping). Buffer zones overlapping land were also cropped to exclude areas over land.

In the absence of telemetry data for Long-tailed Duck and hence reliable data on daily movement patterns, the size of the zone used to determine factors affecting the birds' distribution was based on local winter movement patterns recorded for the Surf Scoter *Melanitta perspicillata*, Lesser Scaup *Aythya affinis* and Greater Scaup *Aythya marila* in San Pablo Bay (Lovvorn *et al.* 2013). Thus, we assumed that Long-tailed Ducks likely would encounter the feeding conditions found within a buffer zone during a feeding period corresponding to the time when birds within this zone were counted. This dataset on bird distribution in relation to bathymetric and food source data is the "modelled dataset" used in the analyses.

In order to support the use of the "modelled dataset" we also performed a parallel analysis where actual *Mytilus* coverage data were used. Here we divided the survey area in a grid of 4 × 4 km cells which, during the data exploratory phase, proved to be the best trade-off between achieving an adequate amount of data within, as well as between, cells. Within each cell we calculated the mean abundance of Long-tailed Ducks, *Mytilus* coverage and the corresponding coefficient of variation. Grid cells containing < 3 observations were excluded. These data are hereafter referred to as the "raw dataset". Methods used for obtaining the raw and modelled data are illustrated in Figure 2. The geographic information systems (GIS) Quantum GIS 1.8.0 Lisboa and ArcMap 9.3, using the coordinate reference system Swedish grid 1990 (RT 90 2.5 gon W), were used to visualise and handle the data.

Statistical modelling

We used a generalized additive mixed model (GAMM) to analyse the dataset with modelled predictors. "Year" was set as a random variable with random intercept allowing mean bird densities to vary randomly across years. Negative binomial regressions (NBs) were used to relate Long-tailed Duck densities (log +1 transformed, hereafter referred to as "Log(Bird abundance $_{\text{modelled}}$ +1)") to habitat variables. NBs were used due to their ability to handle over-dispersion (*i.e.* variance greater than the mean) and excess zeros which, due to the clumped distribution of the ducks, were frequent (Zipkin *et al.* 2014). Bird density (dependent variable) in the raw data (denoted as "Bird abundance$_{\text{raw}}^{0.2}$") was Box-Cox transformed to stabilise variance and a Gaussian distribution was used. Explanatory variables from the modelled dataset were first chosen based on their ecological relevance and later reduced removing all other variables that showed signs of co-linearity (variance infliction factors > 2) and that were deemed redundant based on the Akaike information criterion (AIC). We used a reverse stepwise method,

Table 1. Summary of the generalized additive (mixed) models tested in order to find the most parsimonious model predicting Long-tailed Duck density based on the lowest Akaike information criterion value (AIC). The explanatory variables included in the models were Slope (average slope of the sea bottom), DepthMN (average bottom depth), MytMN:MytCV (the interaction between mean *Mytilus* percentage cover and *Mytilus* coefficient of variation – patchiness) , Long:Lat (the interaction between Longitude and Latitude) and either Year as a fixed (raw data) or random term (modelled data).

Dataset	Model	Explanatory variables	AIC
Modelled	Initial	Slope, DepthMN, MytMN:MytCV, Long:Lat, random(Year)	1,499
		DepthMN, MytMN:MytCV, Long:Lat, random(Year)	1,494
	Final	DepthMN, MytMN:MytCV, random(Year)	1,489
Raw	Final	DepthMN, MytMN:MytCV, Year	428

removing variables from the initial model according to the least significant *P* value. Initial models also included a surface smooth of longitude and latitude to account for spatial autocorrelation between the observations. This term was dropped, however, because it did not improve the AIC, *P* values were affected only marginally, and thus it did not contribute to the overall interpretation of the results (Table 1). All statistical tests were performed using R version 3.1.0 (R Development Core Team 2010) and GAMMs were run using the mgcv package (Wood & Augustin 2002; Wood 2011). Residuals were tested graphically for departures from model assumption (Cleveland 1993).

The most parsimonious models were specified as follows:

(1) $$\text{Log(Bird abundance}_{\text{modelled}} + 1) = \beta + \text{offset(Area)} + \text{s(depthMN)} + \text{s(mytCV, mytMN)} + \text{random(Year)} + \varepsilon$$

(2) $$\text{Bird abundance}^{0.2}_{\text{raw}} = \beta + \text{offset(Area)} + \text{s(depthMN)} + \text{s(mytCV, mytMN)} + \text{Year} + \varepsilon$$

Where β is the overall intercept, *s* is an isotropic smoothing function (thin-plate regression spline, Hastie & Tibshirani 1990) and ε is an error term.

Results

Numbers and distribution of wintering Long-tailed Ducks

During the 1970s, the numbers of Long-tailed Duck wintering in the Hanö Bight was estimated at around 25,000 birds, based on density estimates from boat surveys along linear strip-transects in the area covering 500 m on each side of the ship (Nilsson 1972, 2012). The first of the aerial surveys, in 2007, similarly put the number of Long-tailed Duck in the region at *c.* 23,000, but subsequent estimates were much lower, falling to about 7,000 during the 2011 and 2012 surveys (Fig. 3).

During all surveys the Long-tailed Duck were concentrated mainly in the southern part of the Hanö Bight (Fig. 4). In the northern and especially the northeast part of the area, only small groups were typically found. The same general pattern with some variation was found during all aerial surveys and was also apparent from the survey transects covered by boat in the 1960s and 1970s (Nilsson 1972, 1980a).

Counts from all seven aerial surveys in the Hanö Bight during 2007–2012 were used to calculate the mean densities of Long-tailed Ducks in different parts of the Hanö Bight. In the southern part the density was generally > 20 birds km^{-2}, whereas densities in the northern part generally were around 5–10 birds km^{-2}. Moreover, in the central part of the southern area (Kiviksbredan) mean densities were > 75 birds km^{-2}, with much higher densities recorded on some occasions. Long-tailed Ducks were also present at lower densities south of the Blekinge archipelago and in the deeper outer areas of the Hanö Bight.

Densities in relation to habitat factors

The Long-tailed Ducks were concentrated at depths of between 10–30 m (depthMN, $F_{6.2} = 9.3$, $P < 0.0001$ and $F_{8.9} = 87.6$, $P < 0.0001$ for modelled and raw data sets respectively; Fig. 5 and Fig. 6), even if some flocks were also found in more shallow water. According to Fig. 4, the largest concentration area of the species was found at Kiviksbredan, where the water depth is around 10 m.

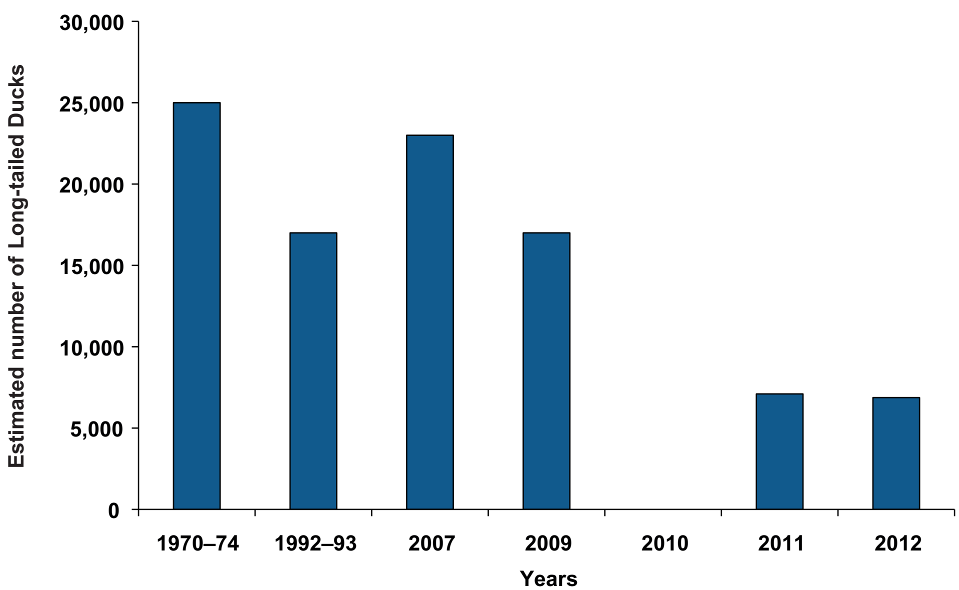

Figure 3. Estimated wintering numbers of Long-tailed Ducks in the Hanö Bight between 1970–74 and 2012.

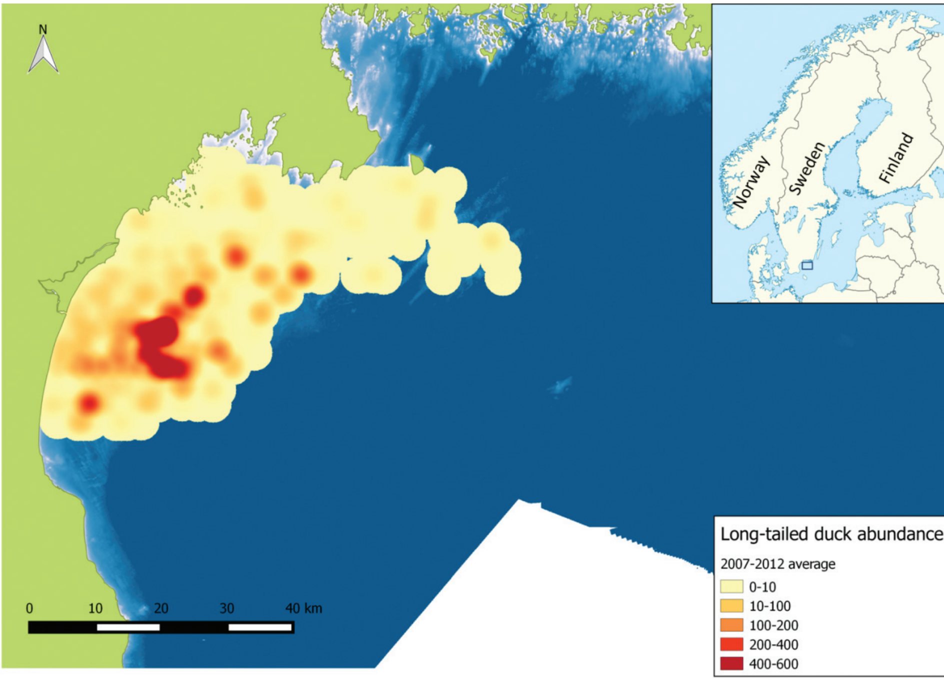

Figure 4. Average Long-tailed Duck abundances between 2007 and 2012.

Mytilus edulis is the main food for the Long-tailed Ducks in the area (Nilsson 1972; Skov *et al.* 2011). Simple comparison of bird densities with *Mytilus* cover revealed considerable variation (Fig. 7), but the highest densities were found in zones with the highest cover of *Mytilus*. *Mytilus* cover was however not the only predictor of Long-tailed Duck abundance. In fact, the variation in *Mytilus* densities also had a significant impact on the models, *i.e.* patchiness of the resource was important as bird densities were negatively correlated with patchiness but the effect varied somewhat for different levels of *Mytilus* coverage (mytCV × mytMN interaction, $F_{5.2} = 6.89$, $P < 0.0001$ and $F_{28.6} = 38.7$, $P < 0.0001$ for modelled and raw data sets, respectively). This effect was fairly consistent across both modelled and raw data (Fig. 8 and Fig. 9). Thus, the abundance of Long-tailed Ducks was generally highest when *Mytilus* coverage was high and even (Figs. 8, 9). The analysis using the larger dataset based on modelled *Mytilus* coverage does however indicate that patchiness had less importance when *Mytilus* was highly abundant and higher importance when *Mytilus* abundance was low (Fig. 8). This pattern was not observed in the model based on raw data (Fig. 9).

Discussion

Our best model predicted that the highest Long-tailed Duck densities would be in areas where water depths to the sea bottom

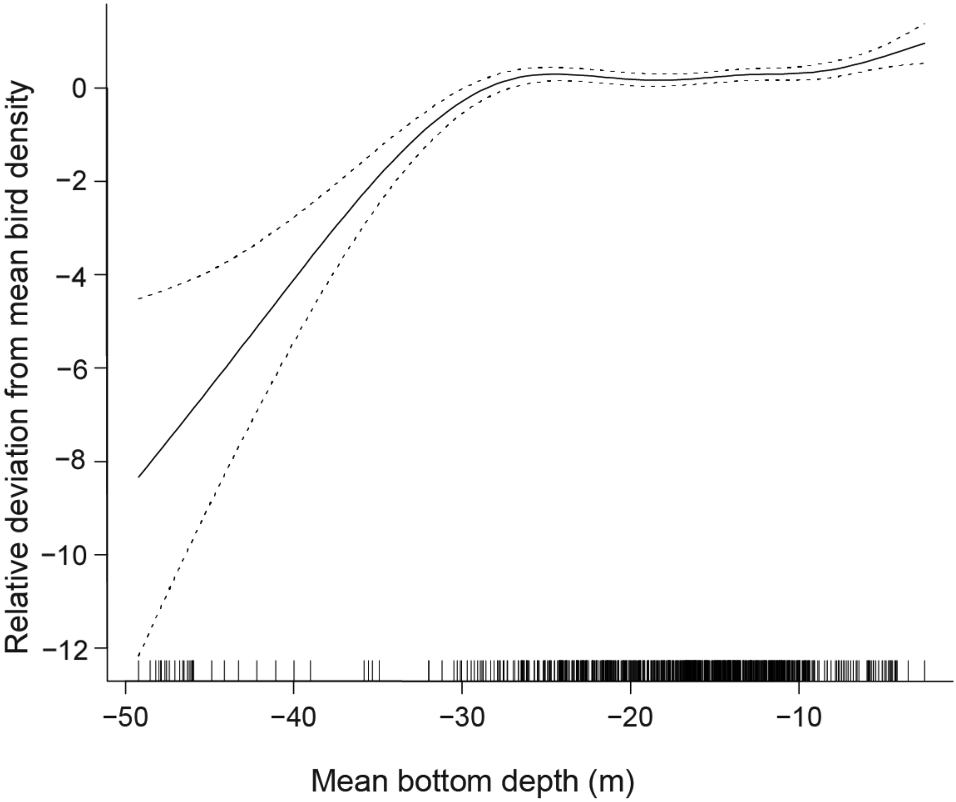

Figure 5. Generalized additive model derived effect of Long-tailed Duck density as a function of mean bottom depth (m) using modelled depth data. The smooth filled line shows relative change in duck density in relation to the mean (0). Dashed lines indicate two standard error bounds.

were 10–30 m in the Hanö Bight (Fig. 5), which corresponded well with their actual distribution over the relatively shallow Kiviksbredan (*cf.* White *et al.* 2009). At these depths, *Mytilus* were common and within diving capacity of the ducks (Nilsson 1972).

While sea depth was the most important variable in explaining the spatial distribution and density of Long-tailed Ducks we also saw a positive relationship between *Mytilus* coverage and Long-tailed Duck densities which is in line with observation from Lithuanian offshore waters (Vaitkus & Bubinas 2001). However, we also found an inverse interaction with patchiness of the resource, where patchiness had a stronger negative effect when the mean density of *Mytilus* was low and less so when *Mytilus* densities were high. This pattern was more pronounced in the modelled data, probably because of the greater geographical coverage and spatial resolution. However, as we lack solid data on the daily foraging areas used by Long-long tailed Ducks, it could be that the observed relationships do not hold

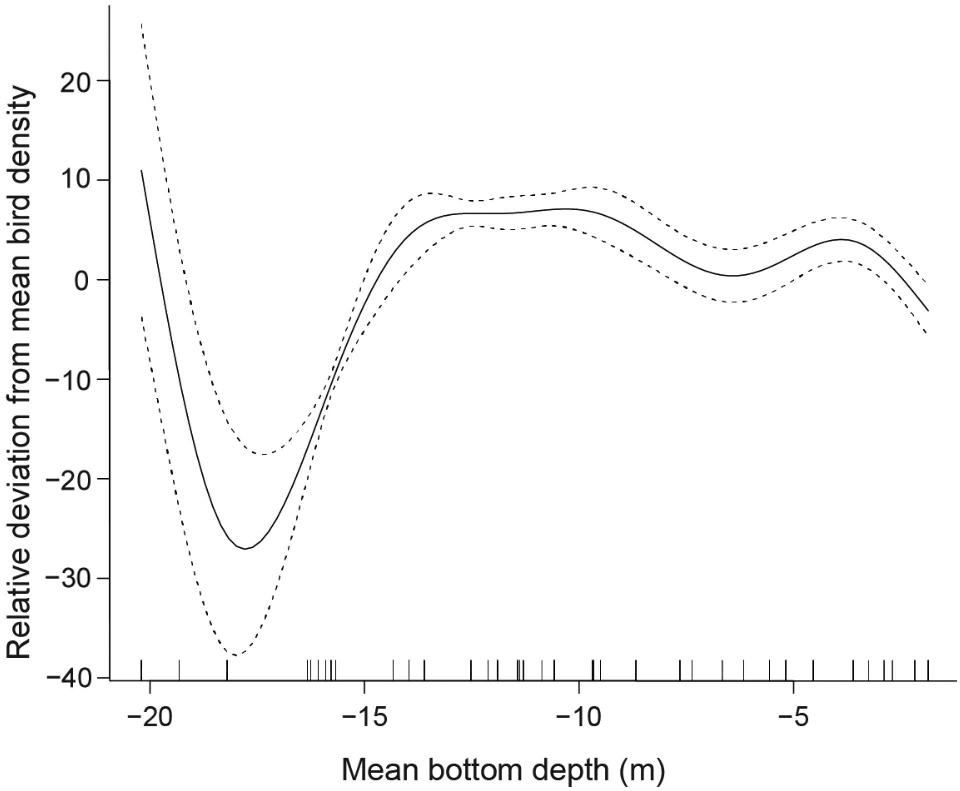

Figure 6. Generalized additive model derived effect of Long-tailed Duck density as a function of mean bottom depth (m) using measured depth data. The smooth filled line shows relative change in duck density in relation to the mean (0). Dashed lines indicate two standard error bounds.

at other spatial scales. Telemetric studies of other diving ducks indicate that their movement patterns fell within the range of the size of buffer zones used in this study (*c.f.* Lovvorn *et al.* 2013), suggesting that the spatial scale applied in our models is reasonable. Moreover, we consider that the validity of our results to be supported by the emergence of similar patterns using different geostatistical approaches and to some extent varying spatial scales. Hence, our results suggest that Long-tailed Ducks choose foraging areas that optimise their energetic gains in line with optimal foraging theory (Pyke 1984; Tome 1988).

It is reasonable to hypothesise that in an energetic context the ducks can afford to forage in an environment that is locally variable if the absolute biomass of the resource is high. Variability on the other hand should become more costly as the availability of the resource decreases, elevating the time invested in searching for prey, thus increasing energetic costs in patchy environments characterised by low overall biomass. Such behaviour is predicted

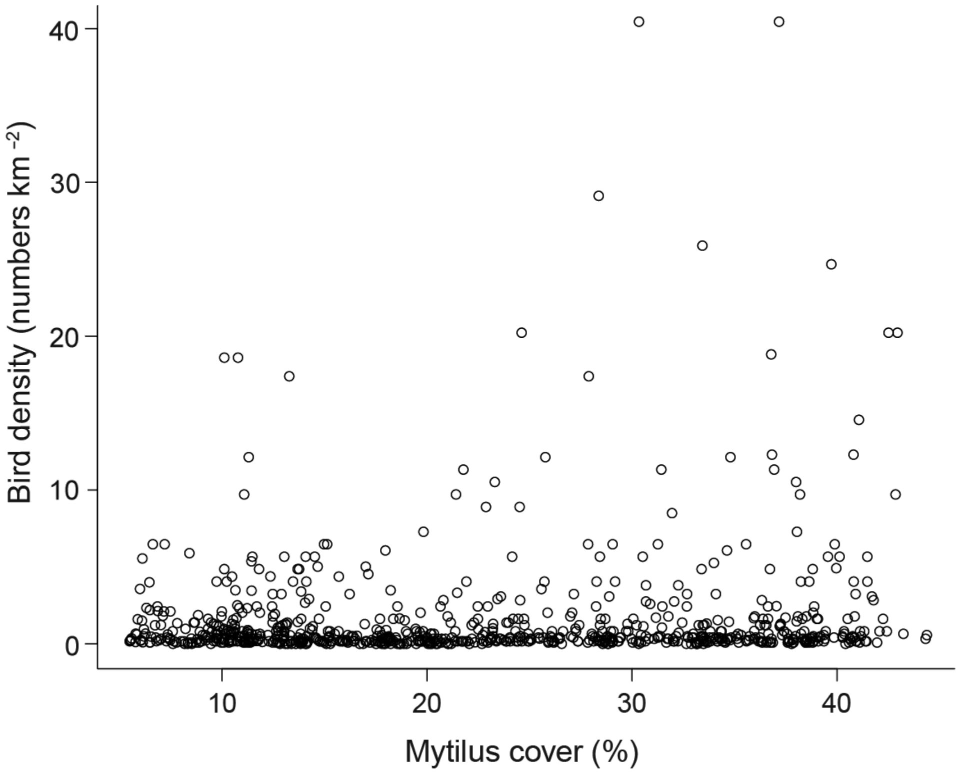

Figure 7. Long-tailed Duck density (numbers km^{-2} as a function of modelled *Mytilus* cover (%).

by the marginal value theorem (Charnov 1976) which states that the time spent by an animal foraging in a patchy environment will increase with increasing quality of a patch or increased distance between patches, and has been demonstrated in a wide range of organisms (Cowie 1977; Cassini *et al.* 1990; Wajnberg *et al.* 2000).

In our study, resource quality was measured as a function of *Mytilus* coverage and patchiness, but energetic optimisation, and hence resource quality, is very much determined by the energy content of the resource as well as the energy spent on handling prey of certain sizes (*cf.* Werner & Hall 1974). It is well known that Long-tailed Ducks show a clear preference for bivalves of a certain size. For instance, Stempniewicz (1995) observed that Long-tailed Ducks preferred 11 mm *Mytilus* and the Baltic Clam *Macoma balthica* in the southern Baltic Sea, and Vaitkus & Bubinas (2001) found that the mean biomass of individual bivalves consumed by Long-tailed Ducks was important in explaining Long-tailed Duck densities in Lithuanian offshore waters. It is therefore very likely that prey size is an important parameter governing the habitat choice of the ducks and one that potentially could introduce variance to the relationships

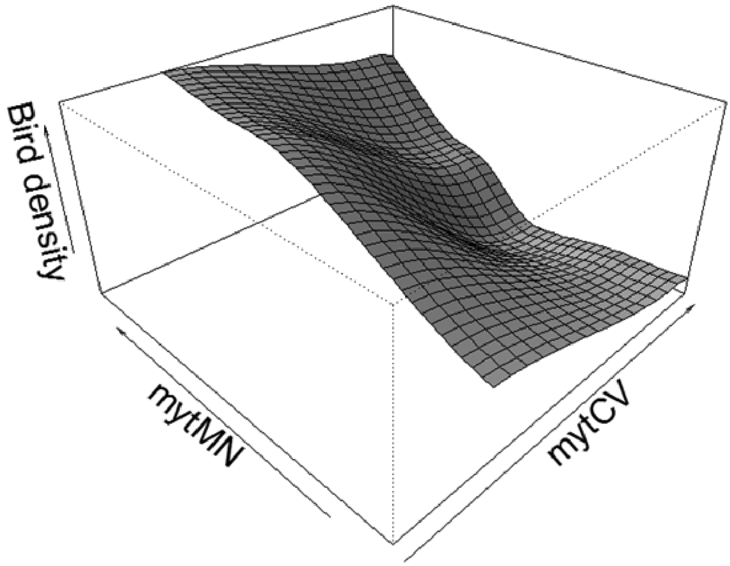

Figure 8. 3D graph showing Long-tailed Duck density (numbers per km^2) as a function of the interaction term between *Mytilus* CV (mytCV) and average *Mytilus* coverage (mytMN) using LOESS smoothing for modelled *Mytilus* data.

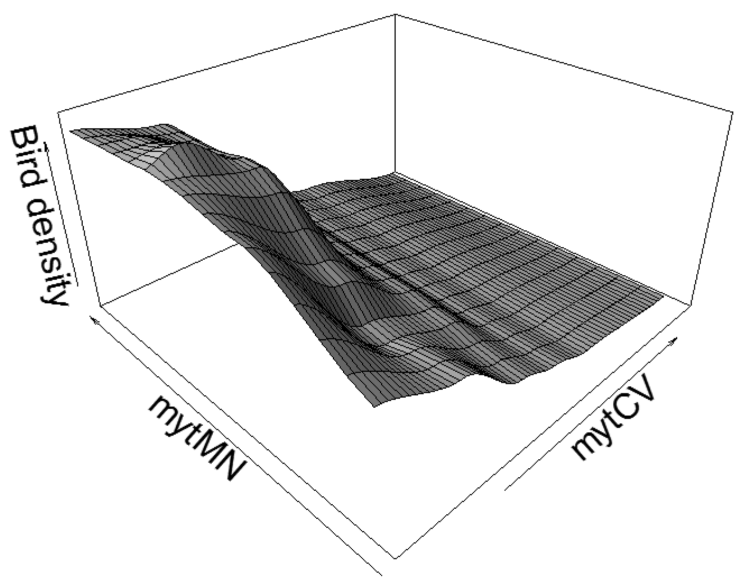

Figure 9. 3D graph showing Long-tailed Duck density as a function of the interaction term between *Mytilus* CV (mytCV) and average *Mytilus* coverage (mytMN) using LOESS smoothing for raw *Mytilus* data.

we have found. In the study by Vaitkus & Bubinas (2001), the authors also identified mollusc diversity as being an important predictor of diving duck abundances. Zydelis & Ruskute (2005) on the other hand, found that Long-tailed Duck overwintering along the Lithuanian coast fed in low quality patches (low density) but on crustaceans of high energetic content, suggesting alternative feeding strategies but both supporting optimal foraging theory. In our case, neither strategy is likely to be important, because the sea bottom in the Hanö Bight, where most Long-tailed Ducks reside, mainly consist of hard substrates and are almost exclusively dominated by *Mytilus* (Ahlman *et al.* 2014), which also is reflected in Long-tailed Duck diets from the area (Nilsson 1972, 1980b).

Recent declines in Long-tailed Duck abundances, and their strong reliance on *Mytilus* as a food source, underlines the need for improved knowledge about their interrelationships. This necessitates the collection of reliable data on *Mytilus* biomass, size class distribution and community composition, as well as Long-tailed Duck foraging preferences, something which is currently not readily available. Moreover, the lack of intra- and inter-annual variation in *Mytilus* distribution and abundance makes it very difficult to factor in the effects of variables that might affect this food source and hence the viability in Long-tailed Duck distribution and abundance.

In conclusion, this study lends support to optimal foraging theory and the marginal value theorem (Charnov 1976) by showing that Long-tailed Ducks chose foraging habitats in a way that optimises their energetic gains, which seems to be a function of prey accessibility (water depth), density (biomass) and patchiness. While the principles of optimal foraging have been demonstrated to hold for many different groups of animals, including diving ducks (*e.g.* Halsey *et al.* 2003), this study is to the best of our knowledge the first of its kind to use field data to show the linkages between Long-tailed Duck habitat choice and resource quality in terms of both prey density and prey availability. However, determining whether the observed relationships hold in other geographical areas where, for instance, the size distribution of *Mytilus* and/or environmental conditions are different requires additional study. We therefore suggest that sites such as Hoburgs Bank and the Midsjö Banks, southwest of Gotland, be investigated further because they are known to be important wintering habitats for Long-tailed Ducks (Nilsson 2012), the bottom substrates as well as the macrobenthic communities have been described in fairly recent times (Naturvårdsverket 2010), and there are plans for the Geological Survey of Sweden to survey these areas again in 2016 (Martin Isaeus, AquaBiota Water Research, pers. comm.).

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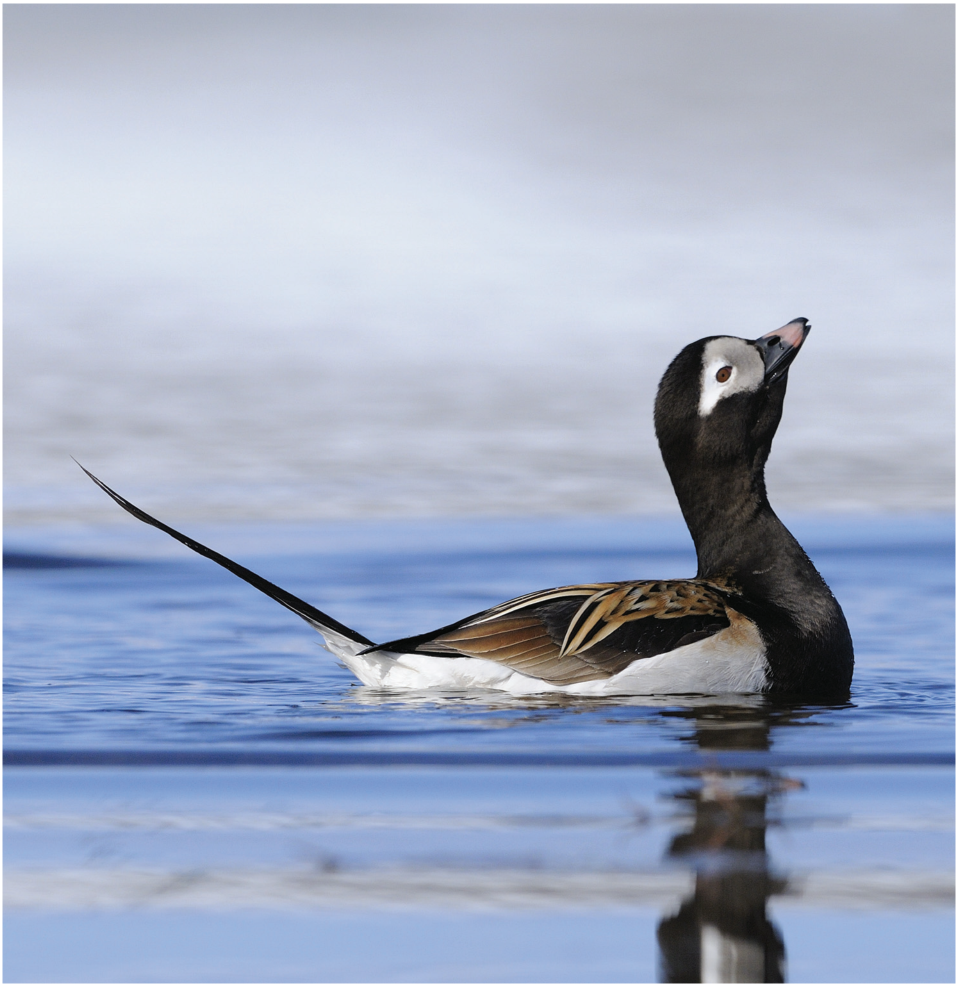

Photograph: Long-tailed Duck (adult male) in breeding plumage, with head raised in courtship display, on the Varanger Peninsula in Norway, by Malcolm Schuyl/FLPA.